

DOI: 10.19615/j.cnki.1000-3118.170627

Restudy of *Regalerpeton weichangensis* (Amphibia: Urodela) from the Lower Cretaceous of Hebei, China

RONG Yu-Fen^{1,2}

(1 Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044 rongyufen@ivpp.ac.cn)

(2 University of Chinese Academy of Sciences Beijing 100049)

Abstract *Regalerpeton weichangensis* was established in 2009 on an incomplete skeleton preserved mainly as an impression from the Lower Cretaceous of Hebei, China. However, several anatomical characters were misinterpreted due to distortion of the holotype, and its taxonomic position has been in debate. In this paper, *R. weichangensis* is redescribed based on eight new specimens and its diagnosis and phylogenetic position are re-examined. This work shows that *R. weichangensis* was a neotenic form with ossified carpals and tarsals. It has a series of unique combination of characteristics including the vomer with a transverse vomerine tooth row, anterior end of the cultriform process of the parasphenoid indented, basibranchial II triradiate and scapulocoracoid with a rectangular coracoid end. Phylogenetic analysis suggests *Regalerpeton*, *Jeholotriton* and *Pangerpeton* should be placed in the suborder Salamandroidea with three synapomorphies. Moreover, they also share uncapitate ribs with Cryptobranchoidea, which indicates that they represent an important stage of evolution in the Cryptobranchoidea-Salamandroidea split.

Key words *Regalerpeton weichangensis*, morphology, phylogeny, Salamandroidea

Citation Rong Y F, in press. Restudy of *Regalerpeton weichangensis* (Amphibia: Urodela) from the Lower Cretaceous of Hebei, China. *Vertebrata Palasiatica*, DOI: 10.19615/j.cnki.1000-3118.170627

1 Introduction

Since the late 1990s, a large number of salamander fossils have successively been unearthed from Jurassic and Cretaceous strata in northeastern China, and eleven taxa have been established: *Laccotriton subsolanus* Gao et al., 1998, *Liaoxitriton zhongjiani* Dong and Wang, 1998, *Jeholotriton paradoxus* Wang, 2000, *Sinerpeton fengshanensis* Gao and Shubin, 2001, *Chunerpeton tianyiensis* Gao and Shubin, 2003, *Liaoxitriton daohugouensis* Wang, 2004, *Pangerpeton sinensis* Wang and Evans, 2006, *Regalerpeton weichangensis* Zhang et al., 2009, *Beiyanerpeton jianpingensis* Gao and Shubin, 2012, and *Qinglongtriton gangouensis* Jia and

国家自然科学基金(批准号: 41472018)和中国科学院战略先导性项目(编号: XDB18030503)资助。

收稿日期: 2017-5-23

Gao, 2016a, *Nuominerpeton aquilonaris* Jia and Gao, 2016b. These taxa provide a rich source of information on primitive salamanders, and are significant in understanding the origin of modern salamander clades. Among these taxa, *R. weichangensis* was erected on an incomplete skeleton preserved mainly as impression. This preservation limited our understanding of its morphology and phylogeny. In the original paper, *Regalerpeton* was placed as the sister taxon of *Chunerpeton* plus living cryptobranchids (Zhang et al., 2009), whereas Skutschas and Gubin (2012) suggested it as a sister taxon of Hynobiidae.

In this paper, eight new specimens which can be referred to *R. weichangensis* are described from northern Hebei Province of China. These better preserved materials permit a revised diagnosis of the taxon and allow a new phylogenetic analysis to be conducted that includes most of the fossil taxa from China.

Abbreviations ac, acetabulum; ad. f, anterodorsal fenestra; am. f, anteromedial fenestra; at, atlas; bb I–II, basibranchial I–II; c, centrale; cb I–II, ceratobranchial I–II; cr vent, crista ventralis; d, dentary; dc, distal carpal; dt 1–3, distal tarsal 1–3; d 1–5, digit 1–5; e+o, exoccipital+opisthotic; fe, femur; fi, fibula; fib, fibulare; fo. i. den, inferior dental foramen; fr, frontal; gf, gill filament; gr, gill raker; hb I–II, hypobranchial I–II; hu, humerus; i, intermedium; il, ilium; in. c. a, internal carotid artery; isc, ischium; lac, lacrimal; m, maxilla; n, nasal; os, orbitosphenoid; p+c, prearticular+coronoid; pa, parietal; ph 2–5, phalanx 2–5; pm, premaxilla; pm. apr, ascending process of the premaxilla; prf, prefrontal; pro, prootic; ps, parasphenoid; pt, pterygoid; qua, quadrate; ra, radius; rad, radiale; sa, sacral; sca, scapulocoracoid; sq, squamosal; st, stapes; ti, tibia; tib, tibiale; ul, ulna; uln, ulnare; vo, vomer; vot, vomerine tooth row.

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.

2 Systematic paleontology

Class Amphibia Linnaeus, 1758

Subclass Lissamphibia Haeckel, 1866

Superorder Caudate Scopoli, 1777

Order Urodela Duméril, 1806

Family Salamandroidea Dunn, 1922

Genus *Regalerpeton* Zhang et al., 2009

Type species *Regalerpeton weichangensis* Zhang et al., 2009.

Holotype IVPP V 14391A, B, an incomplete skeleton impression preserved as part and counterpart on slabs of siltstone.

Referred specimens IVPP V 15677, an incomplete skeleton impression with a nearly complete skull in dorsal view. V 16776A, B, an incomplete skeleton with a nearly complete skull and partial postcranial skeleton that shows well-developed anterodorsal and anteromedial

fenestrae. V 16790A, B, an incomplete skeleton with disarticulated bones of the skull that shows the morphology of the premaxilla, vomer, pterygoid, squamosal and dentary. V 16798A, B, an incomplete skeleton impression with impression of the external gills and ossified carpals. V 17989, a nearly complete skeletal impression with a well-preserved skull in ventral view. V 16802A, B, an incomplete skeletal impression with ossified carpals. V 23342A, B, an incomplete skeletal impression lacking part of the tail, with some bones displaced from their original positions due to lateral compression. V 23343A, B, an incomplete skeleton with disarticulated bones of the skull that shows the morphology of the premaxilla, maxilla, prearticular+coronoid, parasphenoid and ilium.

Revised diagnosis *Regalrpeton weichangensis*, a neotenic salamander, is diagnosed by the following unique combination of characters: premaxilla with a distinct ascending process and bearing approximately 25 teeth; slender maxilla without the facial process and bearing approximately 28 teeth; dentary bearing approximately 40 teeth; nasals without midline contact; anterodorsal and anteromedial fenestrae present; lacrimal and prefrontal present; parietal-prefrontal contact absent; squamosal with two proximal expansions; quadrate ossification present; roughly pentagonal vomer with transversely oriented vomerine tooth row; parasphenoid inverted arrow-shaped with an indented anterior end of the cultriform process; internal carotid foramina penetrating parasphenoid; pterygoid triradiate with a vimineous dentate anterior ramus; paired hypobranchial I and II ossified; basibranchial II triradiate; prearticular and coronoid fused with two processes; opisthotic and exoccipital fused; stapes present; three pairs of external gills present with ossified or calcified gill rakers; 16 presacral vertebrae; atlas with bifid interglenoid tuberosity; trunk vertebrae amphicoelous and ribs uncapitate; three pairs of free postsacral ribs; coracoid portion of scapulocoracoid rectangular; ilium spoon-shaped; humerus with crista ventralis; carpals and tarsals ossified; digit 2 in manus and digit 1 in pes short; phalangeal formulae 2-2-3-2 in manus and 2-2-3-3-2 in pes.

Locality and horizon The specimens of *Regalrpeton weichangensis* are from three different localities (Fig. 1): Daobaziliang, Weichang County, Hebei Province, China (the holotype); Xishunjing village, Weichang County (V 15677, V 16776A, B, V 16790A, B, V 16798A, B, 17989, V 16802A, B, V 23342A, B), and Yulinzi village, Weichang County (V 23343A, B). Dabeigou Formation, Lower Cretaceous (Gao et al., 2013).

Remarks Because of incomplete preservation and distortion of the holotype, several morphological characteristics are absent and misinterpreted. Further, series of reliable characteristics can be concluded as below: the pterygoid is triradiate, with a vimineous dentate anterior ramus. Although the original article is described as two pairs of ceratobranchials due to poor preservation, it is reinterpreted as two pairs of hypobranchials. The coracoid portion of scapulocoracoid is rectangular. In the original article, a detailed discussion about the shape of coracoid portion shows that scapulocoracoid is the identification of the characteristics of *Regalrpeton*. The study of new specimens also agrees that conclusion is reliable. The vomerine tooth row is transversely oriented and vomer is pentagonal. The primitive

interpretation of the orientation is parallel to the maxillary arcade because of distortion of the parasphenoid. New study on the holotype indicates that vomer should be roughly pentagonal. The parasphenoid has prominent cultriform process. The angular is absent in the mandible. The tarsals are ossified. Based on the comparison of the above characteristics combination, the new specimen are referred to *R. weichangensis*.

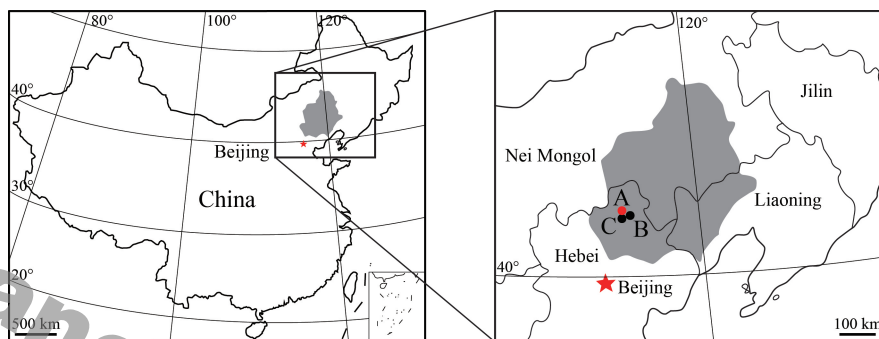


Fig.1 Fossil localities of *Regalerpeton weichangensis* in Hebei, China
The shaded area shows “Jehol Province”, after which the “Jehol Biota” was named
A. Daobaziliang; the locality of the holotype; B. Xishunjing; C. Yulinzi

3 Description

Among the eight new specimens, V 23342 (Figs. 2, 3) is the best preserved. The following description is based on it unless otherwise noted.

Skull roof The skull roof is composed of the paired nasals, lacrimals, prefrontals, frontals and parietals, showing no dermal sculpture.

The nasal (Fig. 4A) is a large triangular bone. It contacts the ascending process of the maxilla anteriorly, frontal posteriorly and prefrontal laterally. It is not connected to the lacrimal. The nasals are separated by a large anterodorsal fenestra (Fig. 4A, C).

The lacrimal is a small quadrilateral bone (V 16798) that forms the posterior edge of the nasal fenestra and the anterior edge of the orbit. The nasolacrimal ducts are not observed due to poor preservation.

The prefrontal (Fig. 4) is a cuneate bone. Its anterior border has inverted V-shape, with the anteromedial side suturing with the nasal and the posterolateral side with the lacrimal. Medially, it contacts the frontal, but not the parietal.

The frontal (Figs. 2, 4A) is a longitudinal bone with a small anterolateral extension. Its anterior border completely contacts nasal. Posteriorly, the frontal overlies the parietal extensively.

The parietal (Figs. 2, 4A) is also a longitudinal bone. It is slightly shorter than frontal and lies posterior to the frontal. The parietal is sutured along the posterior midline, but separated anteriorly by an anteromedial fenestra (Fig. 4A, C). The parietal has a well-developed

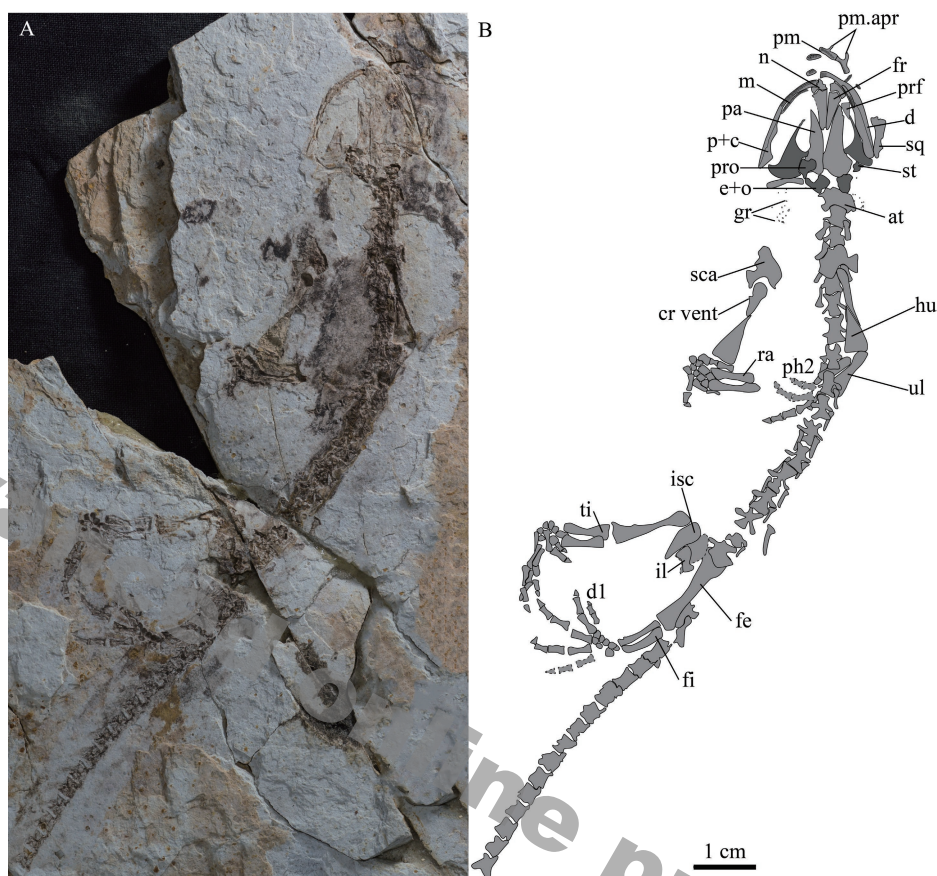


Fig. 2 Photograph (A) and line drawing (B) of *Regalierpeton weichangensis* (IVPP V 23342A) in dorsal view. The frontal bone shows an anterolateral extension along the posterolateral margin of the frontal, but it fails to extend to the prefrontal. Posteriorly, the parietal has an obvious lateral extension that articulates with the squamosal (Fig. 4A). In lateral view, the parietal is seen to articulate with the orbitosphenoid ventrally.

Palate The floor of the skull consists of two completely separated vomers anteriorly and one parasphenoid posteriorly.

The vomer (Figs. 4B, 5B) is roughly pentagonal with a prominent extension laterally. The posterolateral border of the vomer has a slight notch for the choana. There are about 20 teeth (V 17989) in the vomer; they are monostichous and nonpedicellate. The vomerine tooth row (Figs. 4B, 5B) is transversely oriented and runs from the midline towards the lateral extension.

The parasphenoid (Fig. 5D) is a large arrow-shaped bone. The anterior end of the parasphenoid is serrated, including four processes, the medial two of which are cuspidal and the lateral two long and obtuse. The lateral margins of the serrated part have facets for the vomers. Posteriorly, the parasphenoid broadens obviously and has a recognized conule on both sides, for articulating with the orbitosphenoids. There is a groove on each side of the parasphenoid wing, along which the internal carotid artery runs. The orbitosphenoid (sphenethmoid) (Fig. 4B) is approximately cuboid and they ossified to form the lateral side of the neurocranium.

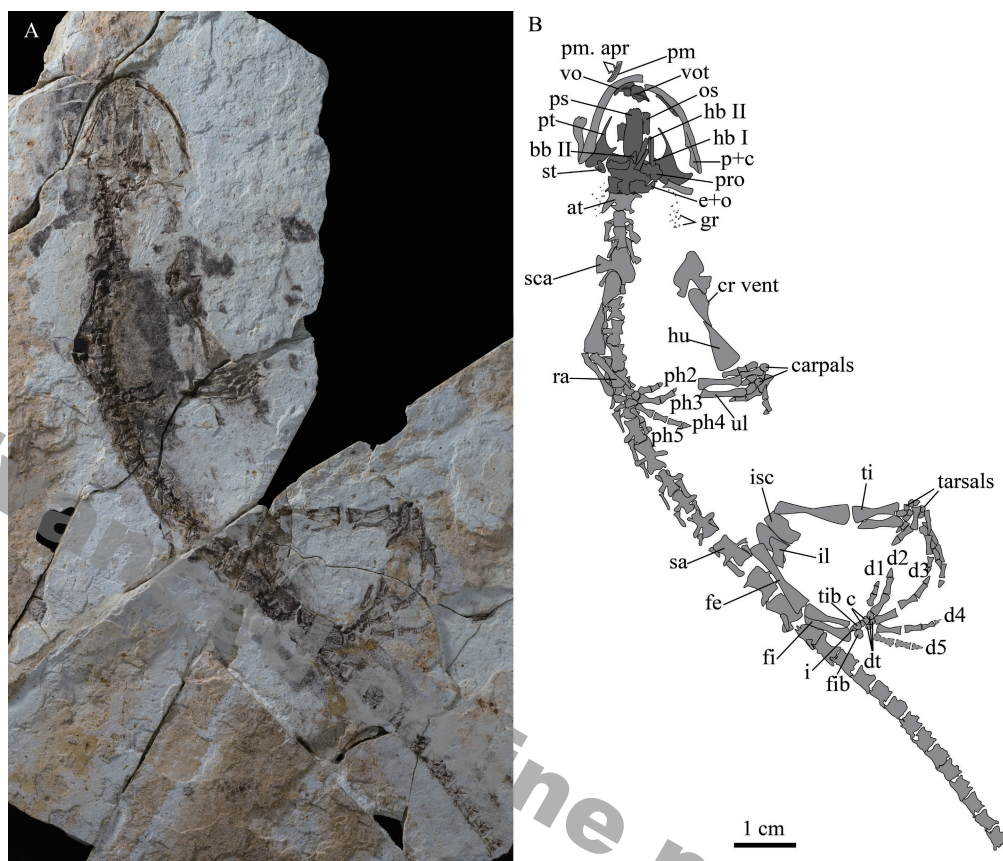


Fig. 3 Photograph (A) and line drawing (B) of *Regalerpeton weichangensis* (IVPP V 23342B) in ventral view

Suspensorium The suspensorium consists of the paired pterygoids, squamosals and quadrates.

The pterygoid (Figs. 3, 4) is triradiate, with a vimineous anteromedial process which is free and curving and has ten teeth. Its posterolateral process articulates with squamosal and quadrate. It has a shorter medial process that points to parasphenoid. There is no contact between the pterygoid and the parasphenoid.

The squamosal (Fig. 4) is a slightly curving lamellate of bone and presents as a transverse bar in the posterior skull. It has two proximal expansions, anterior one smaller than the posterior one. Ventrally, the squamosal articulates with the pterygoid and the quadrate (Fig. 4B).

The quadrate (Fig. 4A, B) is a roughly triangular bone that lies in the ventral surface of the squamosal.

Otico-occipital region The otico-occipital region of *Regalerpeton* consists of three endochondral bones: the prootic, a compound containing opisthotic and exoccipital, and stapes (columella). Both prootic and opisthotic form the anterior and posterior walls of the otic capsule respectively. The stapes (Fig. 3) is nail-shaped, with the head forming the round

footplate and its shaft forming a short stylus. Its footplate covers the lateral wall of the otic capsule. In *Regalerpeton*, opisthotic and exoccipital form a compound which expose completely in the parietal end (Fig. 4A). The opisthotic portion seems to have an obvious expansion on account of deep impression preserved in V 15677 (Fig. 4A). However, more information from otico-occipital region is not observed because most specimens are preserved as impression.

Upper and lower jaws The upper jaw is formed by two dermal bones on each side: the paired dentate premaxillae medially and the paired dentate maxillae posteriorly.

The premaxilla (Figs. 2, 3, 5A) has a distinct ascending process extending along about one-third of the premaxilla near the midline, which contacts the anterior part of the nasal (Fig. 4A). The premaxilla bears approximately 25 teeth that are gracile, pointed and nonpedicellate.

The maxilla (Fig. 4B) is a slender bone that articulates with the premaxilla anteriorly. A distinct facial process is easily observable. The maxilla is slightly longer than the premaxilla and bears approximately 28 teeth which are similar to the premaxillary teeth.

The mandible consists of two distinct dermal bones: the dentary and a compound bone comprising the prearticular and the coronoid. They surround Meckel's cartilage.

The dentary (Fig. 5E) bears approximately 40 teeth on the lingual surface of the lower jaw. The teeth are small, closely packed and nonpedicellate.

The compound of prearticular+coronoid possesses two processes (Figs. 2, 3, 5G). It has a slender extension that runs along the lingual surface of the lower jaw (Fig. 5G). The inferior dental foramen (Fig. 5G) is a conspicuous feature near the posterior of the compound bone and it carried the ramus alveolaris of facial nerve and the alveolar artery (Francis, 1934). The articular and the angular are not visible.

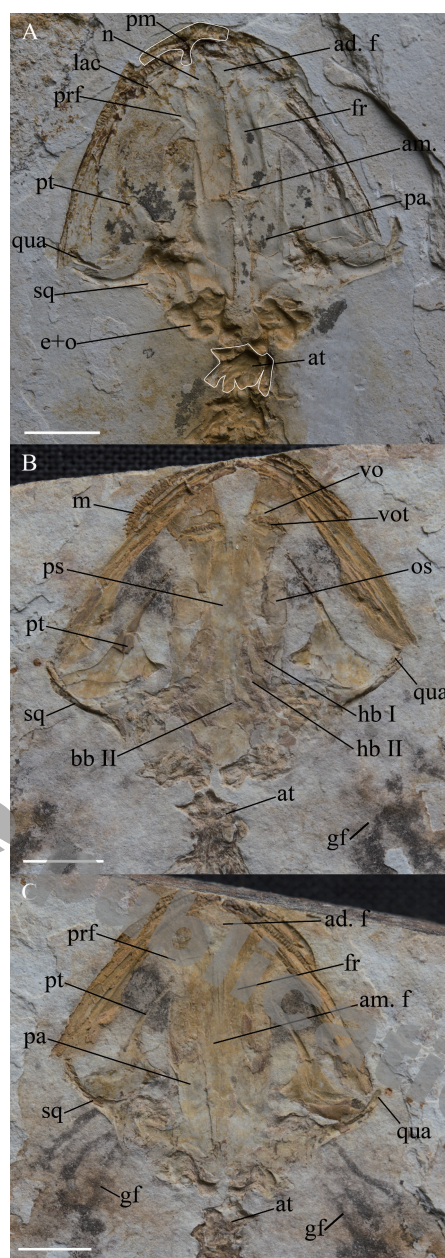


Fig. 4 Photograph of the impression of the skull roof of *Regalerpeton weichangensis* A. IVPP V 15677; B. IVPP V 16776A; C. IVPP V 16776B. Scale bars equal 5 mm



Fig. 5 Skeletons and impressions of *Regalerpeton weichangensis*

Impressions of right premaxilla (A), left ilium (C), parasphenoid (D), left dentary showing articular surface for prearticular + coronoid (F) and left prearticular+coronoid (G); skeletons of right vomer (B), right dentary (E)

A, C, D from IVPP V 23343A; B, E, F from IVPP V 16790B; G from IVPP V 23343B

Hyobranchium The hyobranchium consists of three ossified elements: hypobranchial I, hypobranchial II and basibranchial II (os thyroideum) (Figs. 3, 4B). Hypobranchials I and II are paired, parallel to each other, and each of them is a slightly curved strip. The azygous midline basibranchial II is positioned posterior to other hyobranchial elements and it is triradiate.

Axial skeleton The vertebral column consists of 16 presacrals including the atlas and 15 trunk vertebrae, one sacral, and about 40 caudal vertebrae.

The atlas lacks free ribs and is shorter than the trunk vertebrae. It has two relatively elongated transverse processes (Fig. 4A) and a bifid interglenoid tuberosity (Figs. 4B, C) that articulate with the exoccipitals. All the trunk vertebrae are amphicoelous and all the ribs are uncapitate. The sacral vertebra is larger than the trunk vertebrae, and its ribs are long, thick

and expanded proximally. *Regalerpeton* has a very long tail that exceeds the snout-pelvis length. The first three caudosacrals bear free ribs. The remaining caudal vertebrae lack free ribs, but bear elongate transverse processes, and distinct neural and haemal arches.

Appendicular skeleton The pectoral girdle lies roughly at the level of the 3rd to 4th trunk vertebrae. It consists of only one ossified bone: the scapulocoracoid. The coracoid portion is almost rectangular, and the scapular portion is cuneate.

The humerus is claviform, with expanded proximal and distal portions. In V 23342, the epiphysis of the humerus is wholly ossified and a crista ventralis is present (Figs. 2, 3). The radius is a slender and claviform bone, although the distal portion is inflated. The ulna, which is parallel to the radius, is a slightly curved bone that is longer than the radius (Figs. 2, 3). The carpals are ossified and consist of a radiale, ulnare, intermedium, one centrale, three distal carpals (Fig. 6). There are four digits in the manus and phalanx 2 is very short (V 16776A, B; V 17989). The phalangeal formula is 2-2-3-2.

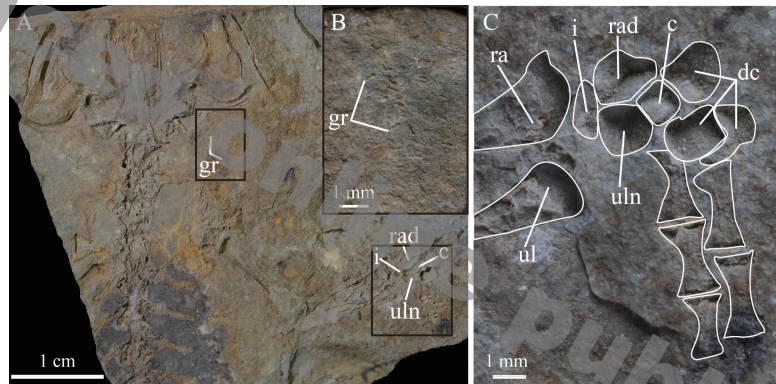


Fig. 6 *Regalerpeton weichangensis* (IVPP V 16802B)

- A. photograph of an incomplete skeletal impression; B. the details of gill rakers;
C. the details of ossified carpals

The pelvic girdle has two ossified elements: a pair of puboischiadic plates ventrally and a pair of ilia laterally. Each puboischiadic plate is approximately blade-shaped and the anterior portion is wider than the posterior one. There is a fossa at the lateral margin of the puboischiadic plate, which together with the ilium, forms the acetabulum. The ilium is a spoon-shaped bone (Fig. 5C). Its proximal portion is expanded and forms part of the acetabulum, while the posterior dorsal portion is slightly curved, and articulates with the sacral rib to attach the pelvic girdle.

The femur (Figs. 2, 3) is a long, straight claviform bone, with the proximal end narrower than the distal one. The tibia and fibula are relative short and straight (Figs. 2, 3). The proximal portion of the tibia is more expanded than the distal end, whereas the fibula is slight curved and its distal portion is relatively inflated. There are seven ossified elements in the ankle (Fig. 3). These consist of the tibiale and fibulare proximally, intermedium, two centralia, and three distal tarsals. There are five digits in the pes. Digit 1 is relatively short (Fig. 2) and the phalangeal formula is 2-2-3-3-2. (Fig. 7)

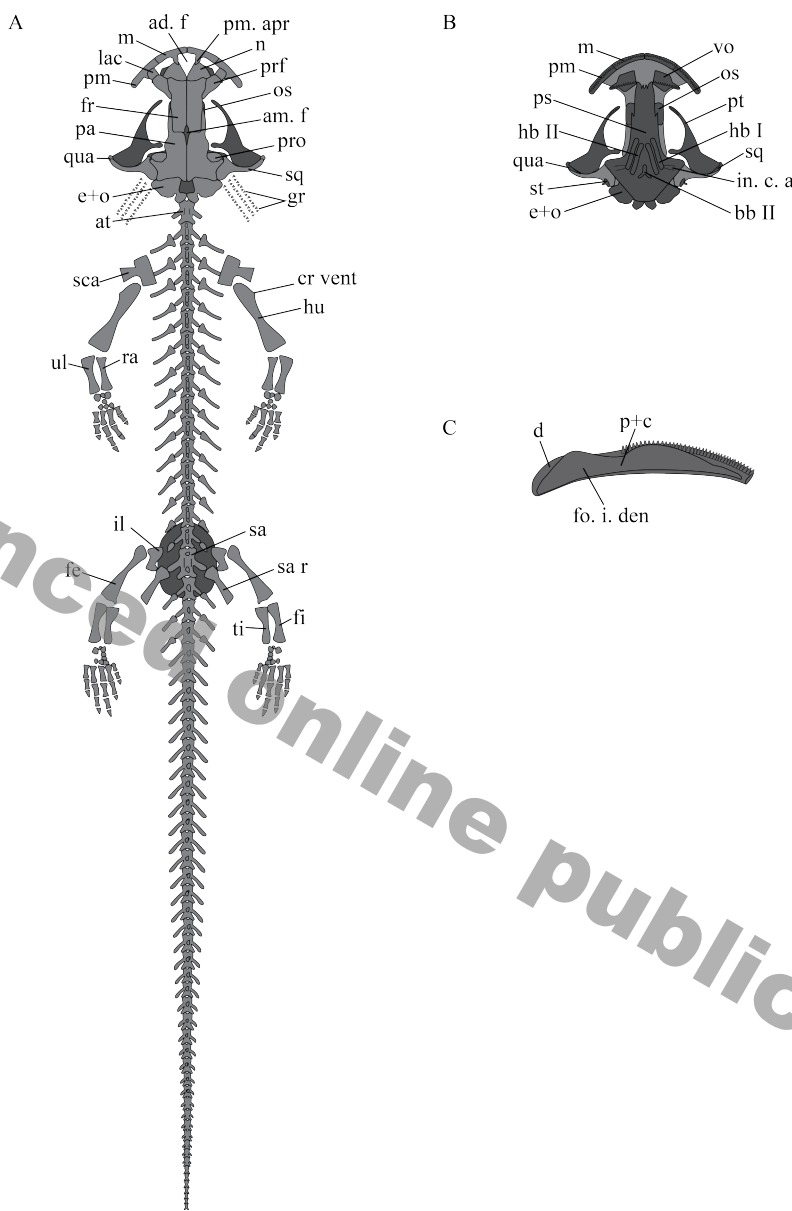


Fig. 7 Reconstruction of the skeleton of *Regalperpeton weichangensis*
A. skeleton in dorsal view; B. skull in ventral view; C. mandible in lingual view. Not to scale

4 Comparison and discussion

4.1 Vomer and vomerine tooth row

The vomer is one of the important dentate elements on the palate for salamanders. The vomerine teeth has played important role in the systematics of salamanders (Fei and Ye, 2017; Regal, 1966; Rose, 2003). In the Cryptobranchidae the vomerine teeth is parallel to the maxillary arcade (Rose, 2003; Qiu and Yang, 1986). In the Hynobiidae the vomerine

teeth varies in length, shape, location and orientation in different genus-species (Fei and Ye, 2017). In the Salamandroidea the vomerine teeth have more complex types such as transverse row along posterior border of the vomer in the Ambystomatidae, teeth covered the posterior extension of the vomer in the Salamandridae and Plethodontidae, vomerine teeth row paralleled to the maxillary arcade in the Proteidae and Amphiumidae (Darda and Wake, 2015; Gregory et al., 2016; Regal, 1966; Rose, 2003).

The vomer of the *Regalperpeton* is roughly pentagonal and the vomerine tooth row is transversely oriented. Compared with other fossil salamanders (Fig. 8), the vomers do not meet each other in the midline, as in *Pangerpeton*, *Seminobatrachus*, *Chunerpeton*, *Jeholotriton* and *Qinglongtriton*. In contrast, a midline contact of the vomers is present in *Liaoxitriton*, *Valdotriton* and *Beiyanerpeton*. Moreover, the pentagonal shape of the vomers is unique in *Regalperpeton*.

In *Chunerpeton*, *Beiyanerpeton*, *Qinglongtriton*, *Seminobatrachus*, and *Valdotriton*, the vomerine tooth row is parallel to the maxillary arcade. In *Jeholotriton paradoxus*, the vomer overgrows the vomerine teeth and has a gracile posterior palatal extension. In *Liaoxitriton daohugouensis*, like *Regalperpeton*, the vomerine teeth row is transverse and medially placed in the palate, but the vomers are larger and of a different shape (Fig. 8). The *Nuominerpeton aquilonaris* (Jia and Gao, 2016b) from the Lower Cretaceous Guanghua Formation of Nei Mongol, China, differs from *Regalperpeton* in having a *Liaoxitriton*-like vomer with short multiple rows of vomerine teeth.

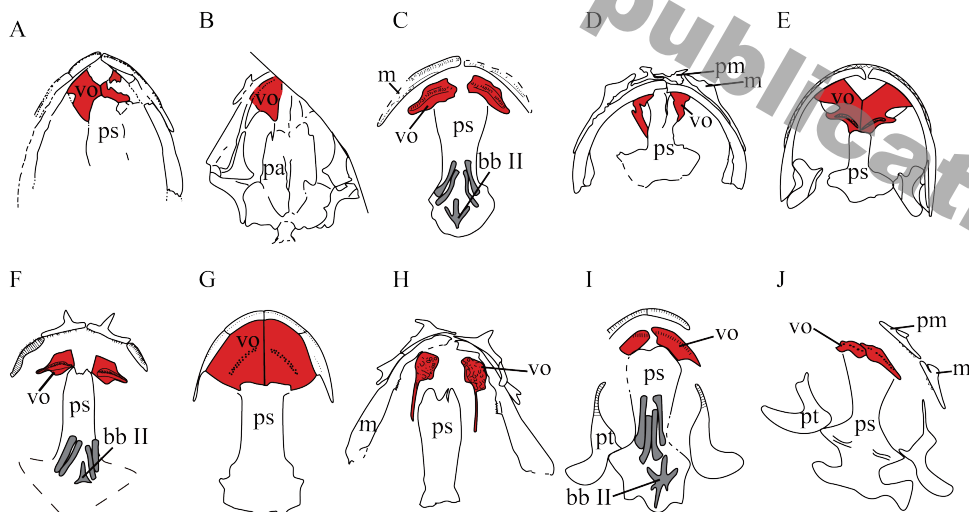


Fig. 8 Comparison of vomer and vomerine tooth row of the fossil salamanders

A. *Liaoxitriton zhongjiani* (Dong and Wang, 1998); B. *Seminobatrachus boltyschkensis* (Skutschas and Gubin, 2012); C. *Chunerpeton tianyiensis* (Gao and Shubin, 2003); D. *Pangerpeton sinensis* (Wang and Evans, 2006); E. *Liaoxitriton daohugouensis* (Wang, 2004); F. *Regalperpeton weichangensis* (IVPP V 17989); G. *Valdotriton* (reconstruction) (Evans and Milner, 1996); H. *Jeholotriton paradoxus* (Wang, 2000); I. *Qinglongtriton gangouensis* (Jia and Gao, 2016a); J. *Beiyanerpeton jianpinggensis* (Gao and Shubin, 2012). Not to scale

4.2 Parasphenoid

In most salamanders, the shape of anterior border of the parasphenoid cannot be well displayed because it is covered with vomers (Fei and Ye, 2017; Darda and Wake, 2015; Gregory et al., 2016; Regal, 1966; Rose, 2003). In *Regalierpeton*, parasphenoid is fully exposed in the palate of the skull on account of separated vomer. It is clearly shown that *Regalierpeton* has an arrow-shaped parasphenoid with an indented anterior end. Other than this taxon, this type is only known in *Liaoxitriton daohugouensis* (Fig. 8), which has a relatively shorter anterior process. Besides, it is unique that parasphenoid has an indented anterior end of the cultriform process. The special morphology of the parasphenoid can be used as the identification feature of *Regalierpeton*.

4.3 Hyobranchium

The hyobranchium lies in the floor of the mouth and supports the tongue. It varies in its configuration in different species (Table 1). In *Chunerpeton*, *Beiynerpeton*, *Qinglongtriton*, and *Regalierpeton*, the hyobranchium consists of ossified hypobranchial I, hypobranchial II and basibranchial II, but the shape of basibranchial II differs among these taxa (Fig. 8). It is triradiate in *Regalierpeton*. However, in *Beiynerpeton*, basibranchial I and II are co-ossified to form a trident-shaped element with slender arms extending anteriorly and anterolaterally (Gao and Shubin, 2012). In *Chunerpeton*, basibranchial II is trident-shaped (Gao and Shubin, 2003), whereas in *Qinglongtriton*, it is more complex in shape, with paired anterolateral and posterolateral processes fused to a median rod (Jia and Gao, 2016a). In modern salamanders, the paired ossified hypobranchial I and hypobranchial II and paralleled to each other, this occurs in the larval and neotenic salamanders like *Andrias davidianus*, *Siren intermedia*, *Pachyhynobius shangchengensis*, *Batrachuperus mustersi*, *Pseudobranchius striatus*, *Proteus anguinus*, *Amphiuma means*, *Desmognathus aeneus* (Qiu and Yang, 1986; Rose, 2003; Xiong

Table 1 The ossified elements of the hyobranchium in different fossil taxa

Taxa	Ceratobranchial	Hypobranchial	Basibranchial
<i>Kokartus honorarius</i>	0	hb I, hb II	0
<i>Laccotriton subsolanus</i>	?	?	bb II
<i>Liaoxitriton zhongjiani</i>	cb I	?	?
<i>Jeholotriton paradoxus</i>	0 ?	0?	0?
<i>Sinerpeton fengshanensis</i>	cb II	?	?
<i>Chunerpeton tianyiensis</i>	0	hb I, hb II	bb II
<i>Liaoxitriton daohugouensis</i>	cb I	hb I	bb II
<i>Pangerpeton sinensis</i>	cb I, cb II	0	0
<i>Regalierpeton weichangensis</i>	0	hb I, hb II	bb II
<i>Beiynerpeton jianpingensis</i>	0	hb I, hb II	bb I + bb II
<i>Qinglongtriton gangouensis</i>	0	hb I, hb II	bb II
<i>Nuominerpeton aquilonaris</i>	cb II	hb II	bb II

Information on the elements of hyobranchium was taken from the literature (*Kokartus honorarius*, Skutschas and Martin, 2011; *Laccotriton subsolanus*, Gao et al., 1998; *Liaoxitriton zhongjiani*, Dong and Wang, 1998; *Jeholotriton paradoxus*, Wang, 2000; *Sinerpeton fengshanensis*, Gao and Shubin, 2001; *Chunerpeton tianyiensis*, Gao and Shubin, 2003; *Liaoxitriton daohugouensis*, Wang, 2004; *Pangerpeton sinensis*, Wang and Evans, 2006; *Beiynerpeton jianpingensis*, Gao and Shubin, 2012; *Qinglongtriton gangouensis*, Jia and Gao, 2016a; *Nuominerpeton aquilonaris*, Jia and Gao, 2016b).

et al., 2013; Deban and Wake, 2000). Accordingly, pairs of hypobranchial I and hypobranchial II present in fossil taxon are considered larval hyobranchium.

4.4 Neoteny

In salamanders, neoteny is a phenomenon in which an animal retains the larval configuration while attaining reproductive maturity (Pierce and Smith, 1979; Shaffer, 2013). There are gill filament impressions (three pairs) (Fig. 4B, C) and ossified or calcified gill rakers (Figs. 2, 3, 6) present in our newly discovered specimens. As in modern relatives, the gill filaments or rakers are indicative of external gills. *Regalerpeton* must therefore have been neotenic, as the adult individuals have 1) external gills; 2) larval-shaped pterygoids; 3) a larval hyobranchium. *Regalerpeton* therefore resembles *Chunerpeton* (Gao and Shubin, 2003), *Beiynerpeton* (Gao and Shubin, 2012) and *Qinglongtriton* (Jia and Gao, 2016a). However, *Regalerpeton* differs from the other three taxa in having the carpals and tarsals fully ossified in the adult stage. It is implied that *Regalerpeton* shows a tendency of more terrestrial life.

5 Phylogenetic analysis

In order to determine the phylogenetic position of *Regalerpeton*, it is added into the latest data matrix of caudates as show in Jia and Gao (2016a). The character states of *Jeholotriton* were also added based on descriptions in Wang (2000), Wang and Rose (2005) and Carroll et al. (2012). Some character states of *Pangerpeton* were modified by re-examination of the holotype (see Appendix 1). *Karaurus* was the designated outgroup taxon, and all the characters were unordered and unweighted as in Jia and Gao (2016a).

The implicit enumeration search algorithm using TNT (Goloboff and Catalano, 2016) resulted in fifteen most parsimonious trees (tree length=263 steps, consistency index=0.464, retention index=0.702). 50% majority rule consensus of 15 most parsimonious trees (Fig. 9) suggests that *Jeholotriton* and *Pangerpeton* are sister taxa with three synapomorphies: vomer with greatly elongated process extending along lateral border of parasphenoid [character state 13(2)]; ossified hypobranchial I absent [character state 33(1)]; pterygoid without teeth [character state 39(0)]. *Regalerpeton* forms a sister taxon to the “*Jeholotriton*+*Pangerpeton*” clade. The analysis also reveals that *Regalerpeton*, *Jeholotriton*, *Pangerpeton*, *Qinglongtriton* and *Beiynerpeton* together form a clade that is sister-taxon to the rest of Salamandroidea. This sister clade is supported by three synapomorphies: ossified nasal without midline contact [character state 8(1)]; angular fused to prearticular [character state 26(1)]; articular absent or by fusion with prearticular [character state 29(1)]. Besides, *Regalerpeton*, *Jeholotriton* and *Pangerpeton* (from the Early Cretaceous of Hebei, Middle/Late Jurassic of Nei Mongol and Liaoning, respectively) share uncapitate ribs with the suborder Cryptobranchoidea. This is in accordance with their transitional position between Cryptobranchoidea and Salamandroidea, which indicates that the two groups may have started to split in the Middle to Late Jurassic. There is also mitochondrial genomes evidence showing the Cryptobranchoidea-Salamandroidea

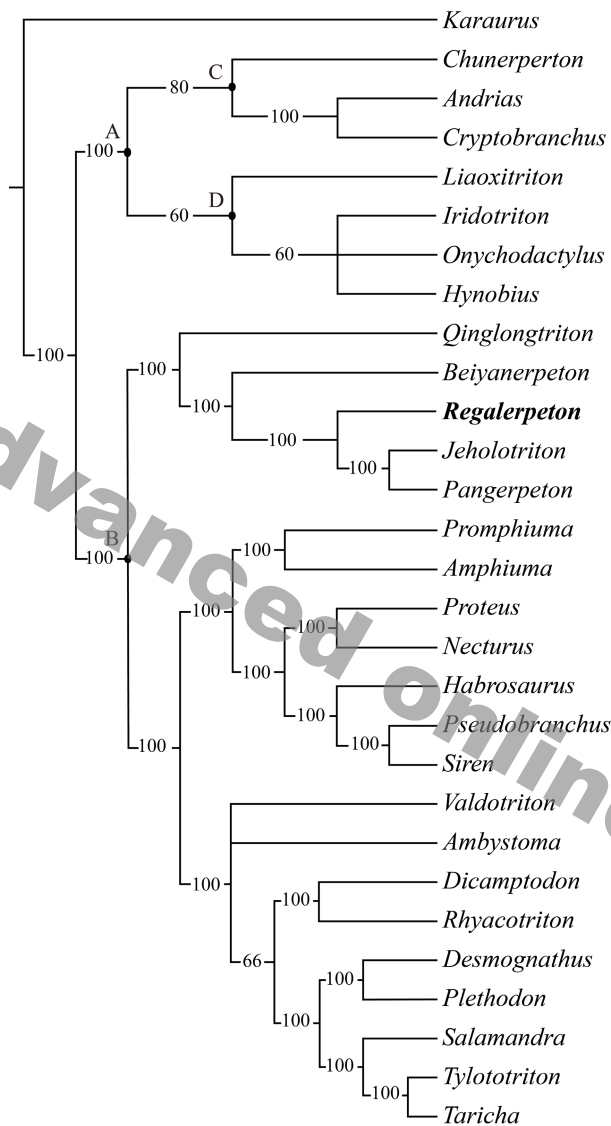


Fig. 9 50% majority rule consensus tree of the most parsimonious trees obtained in TNT (Goloboff and Catalano, 2016) for caudate phylogeny
Clade A. Cryptobranchioidea; B. Salamandroidea;
C. Cryptobranchidae; D. Hynobiidae

split in the Mid-Jurassic (~171 mya) (Zhang and Wake, 2009). Therefore, *Regalerpeton*, *Jeholotriton* and *Pangerpeton* represent an important stage of evolution in the history of salamanders.

6 Conclusions

The following conclusions can be drawn from this study:

1) *R. weichangensis* differs from other salamanders mainly in the following characteristics: it is a neotenic salamander with ossified carpals and tarsals; roughly pentagonal vomer with transversely oriented vomerine tooth row; presence of triradiate basibranchial II; parasphenoid inverted arrow-shaped with an indented anterior end of the cultriform process; coracoid portion of scapulocoracoid rectangular. These features support the generic distinction of *Regalerpeton*; 2) New phylogenetic analysis places *Regalerpeton*, *Jeholotriton* and *Pangerpeton* into the suborder Salamandroidea. They also share unicapitate ribs with Cryptobranchioidea, so the three taxa *Regalerpeton*, *Jeholotriton* and *Pangerpeton* represent an important transitional stage in the evolution of salamanders.

Acknowledgments Thanks to Dr. Dong Liping for discussions on the phylogenetic analysis and Mr. Zhang Shaoguang for taking photographs. I am grateful for my MSc advisor Prof. Wang Yuan for his support and revisions of early versions of this manuscript. Thanks also to reviewers Profs. Susan Evans (UCL), Liu Jun (IVPP) and Chen Jianye (AMNH) for their constructive revisions on the paper. This work was supported by grants from the NNSF of China (grant no. 41472018) and the Chinese Academy of Sciences (grant no. XDB18030503).

河北围场下白垩统围场皇家蜥(*Regalerpeton weichangensis*) (两栖类：有尾类)的再研究

戎钰芬^{1,2}

(1中国科学院古脊椎动物与古人类研究所, 中国科学院脊椎动物演化与人类起源重点实验室 北京 100044)

(2中国科学院大学 北京 100049)

摘要：围场皇家蜥(*Regalerpeton weichangensis*)于2009年基于一件产自河北围场下白垩统不完整的骨骼印痕标本命名。然而由于标本变形导致皇家蜥的部分解剖学特征被曲解，系统发育位置也存在争论。本文基于八件新标本对该蜥的鉴定特征和系统发育位置进行了修订。研究显示，皇家蜥是一种腕骨和跗骨骨化的幼态持续型蜥，具有独特的特征组合，包括犁骨齿列横向排列、副蝶骨前端呈齿状、基鳃骨II呈三射型以及肩胛乌喙骨的乌喙端呈矩形。新的系统发育分析根据三个近裔共性将围场皇家蜥、热河蜥和胖蜥归入蜥亚目。此外，它们还与隐鳃蜥亚目共有“肋骨单关节头”这一特征，显示这三种蜥可能代表了隐鳃蜥亚目与蜥亚目分离时期这一重要演化阶段。

关键词：围场皇家蜥，形态学，系统发育学，蜥亚目

References

- Carroll R, Zheng A, 2012. A neotenic salamander, *Jeholotriton paradoxus*, from the Daohugou Beds in Inner Mongolia. *Zool J Linn Soc*, 164(3): 659–668
- Darda D M, Wake D B, 2015. Osteological variation among extreme morphological forms in the Mexican salamander genus *Chiropterotriton* (Amphibia: Plethodontidae): morphological evolution and homoplasy. *Plos One*, 10(6): e0127248
- Deban S M, Wake D B, 2000. Aquatic feeding in salamanders. In: Schwenk K ed. *Feeding: Form, Function and Evolution in Tetrapod Vertebrates*. San Diego, California: Acad Press. 65–94
- Dong Z M, Wang Y, 1998. A new urodele (*Liaoxitriton zhongjiani* gen. et sp. nov.) from the Early Cretaceous of western Liaoning Province, China. *Vert Palasiat*, 36(2): 159–172
- Evans S E, Milner A R, 1996. A metamorphosed salamander from the Early Cretaceous of Las Hoyas, Spain. *P Roy Soc B-Biol Sci*, 351(1340): 627–646
- Fei L, Ye Y C, 2017. *Amphibians of China I*. Beijing: The Science Publishing Company. 1–1040
- Francis E T B, 1934. *The Anatomy of the Salamander*. Oxford: Clarendon Press. 1–381
- Gao K Q, Shubin N H, 2003. Earliest known crown-group salamanders. *Nature*, 422(6930): 421–424
- Gao K Q, Shubin N H, 2001. Late Jurassic salamanders from northern China. *Nature*, 410(6828): 574–577
- Gao K Q, Shubin N H, 2012. Late Jurassic salamandroid from western Liaoning, China. *Proc Natl Acad Sci USA*, 109(15): 5767–5772

chinaXiv:201708.00331v1

Advanced Online Publication

- Gao K Q, Cheng Z W, Xu X, 1998. First report of a Mesozoic urodele from China. *Chin Geol*, 248(1): 40–41
- Gao K Q, Chen J Y, Jia J, 2013. Taxonomic diversity, stratigraphic range, and exceptional preservation. *Can J Earth Sci*, 50(3): 255–267
- Goloboff PA, Catalano S, 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, 32(3): 221–238
- Gregory A L, Sears B R, Wooten J A et al., 2016. Evolution of dentition in salamanders: relative roles of phylogeny and diet. *Biol J Linn Soc*, 119(4): 960–973
- Jia J, Gao K Q, 2016a. A new basal salamandroid (Amphibia, Urodela) from the Late Jurassic of Qinglong, Hebei Province, China. *Plos One*, 11(5): e0153834
- Jia J, Gao K Q, 2016b. A new hynobiid-like salamander (Amphibia, Urodela) from Inner Mongolia, China, provides a rare case study of developmental features in an Early Cretaceous fossil urodele. *Peer J*, 4(10): e2499
- Pierce B A, Smith H M, 1979. Neoteny or paedogenesis? *J Herpetol*, 13(1): 119–121
- Qiu Y X, Yang A F, 1986. Studies on the osteology of *Andrias davidianus* (Amphibia: Caudata). *Acta Sci Nat Univ Pekin*, (6): 71–89
- Regal P J, 1966. Feeding specializations and the classification of terrestrial salamanders. *Evolution*, 20(3): 392–407
- Rose C S, 2003. The developmental morphology of salamander skulls. In: Heatwole H, Davies M eds. *Amphibian Biology*. New South Wales: Surrey Beatty and Sons. 1684–1781
- Shaffer H B, 2013. Neoteny brenners encyclopedia of genetics, 317(5): 26–27
- Skutschas P P, Gubin Y M, 2012. A new salamander from the Late Paleocene—Early Eocene of Ukraine. *Acta Palaeont Pol*, 57(1): 135–148
- Skutschas P P, Martin T, 2011. Cranial anatomy of the stem salamander *Kokartus honorarius* (Amphibia: Caudata) from the Middle Jurassic of Kyrgyzstan. *Zool J Linn Soc*, 161(4): 816–838
- Wang Y, 2000. A new salamander (Amphibia: Caudate) from the Early Cretaceous Jehol Biota. *Vert Palasiat*, 38(2): 100–103
- Wang Y, 2004. A new Mesozoic caudate (*Liaoxitriton daohugouensis* sp. nov.) from Inner Mongolia, China. *Chin Sci Bull*, 49(8): 858–860
- Wang Y, Evans S E, 2006. A new short-bodied salamander from the Upper Jurassic/Lower Cretaceous of China. *Acta Palaeont Pol*, 51(1): 127–130
- Wang Y, Rose C S, 2005. *Jeholotriton paradoxus* (Amphibia: Caudata) from the Lower Cretaceous of southeastern Inner Mongolia, China. *J Vert Paleont*, 25(3): 523–532
- Xiong J L, Sun P, Zhang J L et al., 2013. A comparative study of the hyobranchial apparatus in Hynobiidae (Amphibia: Urodela). *Zoology*, 116(2): 99–105
- Zhang G, Wang Y, Jones M E H et al., 2009. A new Early Cretaceous salamander (*Regalerpeton weichangensis* gen. et sp. nov.) from the Huajiyang Formation of northeastern China. *Cretaceous Res*, 30(3): 551–558
- Zhang P, Wake D B, 2009. Higher-level salamander relationships and divergence dates inferred from complete mitochondrial genomes. *Mol Phylogenet Evol*, 53(2): 492–508